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Homogeneity of plant communities

by

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A plant community is a group of individuals of plant species, the composition of which being determined by the ecological conditions and by the mutual reactions of the plants.

Ecological conditions greatly influence the composition of the vegetation, quantitatively as well as qualitatively. Where the ecological conditions are varying discontinously and the discontinuities are great enough to cause essential changes in the vegetation, the discontinuities of vegetation naturally coincide with those of the ecological conditions. But even, where no discontinuities of the ecological conditions can be found, discontinuities in the vegetation occur. These discontinuities are caused by competition especially between the dominating species of the communities in question. The borders between such communities are determined by the competive properties of the dominating species and by their ability to influence their own milieu. By the latest action discontinuities also in the ecological conditions are later developed. These also contributes to make the borders between the plant communities more distinct.

It is accordingly to be expected that in cases where ecological conditions of importance to the distribution of the plant communities may be subject to the influence of the plant species, the borders between the different communities will be distinct. In cases where the ecological conditions governing the distribution of the plant communities hardly can be influenced by the plants, the borders must be expected to be more diffuse (e. g. many lacustrine vegetation types).

There is no doubt that the plants take an active part in forming their own milieu. One of the most interesting examples of this is given by Kozlowska (1934) who has shown that the plants by their roots are able to change the acidity of the substratum usually in direction of their optimum acidity. Another factor of importance is the production of debris by the plants which plays an important role by the soil formation.

Competition, struggle for life, doubtlessly is of great importance in the formation of plant communities, and has by some authors been taken as the single basis. This action is in its nature negative, it is only able to exclude species of the plant communities or reduce the vitality of certain species. But one ought not overlook the possibility that the plants, by their formation of their own milieu, and by excluding some species from the community, may favour other plant species (cf. HADAČ 1944, 1947). Proofs of competition between individuals of plant species are found easily enough. But about the nature of competition less is known. The means and methods are fairly well known from the bacteria (cf. HADAČ and JÍCHA 1947) from the different kinds of Penicillium (SLÁNSKÁ 1949) and from the lichens (see e. g. DEGELIUS 1940). These are partly of a mechanical, but also, of a chemical nature. About the means of competition of the higher plants little is known. It is often said that they are principally of mechanical nature, but some facts (cf. RUSSEL 1927, OSVALD 1947, HADAČ 1947) indicate that they are also of a chemical nature. AALTONEN (1923) emphasizes that the roots are most important in this struggle.

In a limited space only a limited number of full grown individuals of a species can exist. Well known is an example pointed out by BRAUN-BLANQUET (1928). In 1 m^2 he found in the spring 2000 seedlings of *Suaeda maritima*. In the autumn only 6—8 fructificating individuals were found in the same area. The power of competition of fullgrown individuals of one species must be assumed to be of approximately the same order of value. Thus in an area with nearly the same ecological conditions all over the area, the fullgrown individuals of one species will each require almost the same area for themselves. Different species will have different possibility to exploit different layers of the soil, and each fullgrown individual will require a living space of a certain size in competition with other individuals of the same species. As a consequence we find communities in which the individuals of the dominating species have almost the same density within different parts of the communities. Such an area is called homogeneous, a concept of fundamental importance to phytosociology (NORDHAGEN 1928). The homogeneity is at least in part due to competition.

The area which each individual of a plant species must have for itself depends upon the specific requirement of the plant of nutrient salts, on the fertility of the soil and on the microclimatical conditions. The most important factor is the fertility of the soil which perhaps will be possible to estimate by means of the density of individuals of a certain species in stabilized plant communities.

Within a homogenous plant community, statistical calculations may be carried out. But for this purpose it is necessary to give a more exact definition what is meant by homogeneity. A plant species is said to be homogeneously distributed within a certain area if the probability to catch an individual of a plant species within a test area of given size is the same in all parts of the area. A plant community is said to be homogeneous if the individuals of the plant species which we use for the characterization of the community are homogeneously distributed.

In nature plant communities are never fully homogeneous, i. e. the density of the species of importance by the characterization of the community, especially the dominating species, have not exactly the same density in all parts of the area. We may thus talk of more or less homogeneous plant communities. Measurements on the homogeneity of the plant communities are rarely carried out, but the human eye, badly adapted to measurement but well to comparison, rapidly gives the trained sociologist an impression whether a plant community he has before his eyes is highly homogeneous or not.

There is, after the definition of homogeneity given above, many types of distribution which may be called homogeneous. The individuals of the species in question may be distributed at random (normal dispersion). What is meant by distribution at random will appear from the following developments. Or the individuals may be quite regularily distributed like the gitterpoints of a quadratic gitter. Or the individuals may occur in aggregates which in turn are distributed at random.

For the statistical treatment of the problems of the distribution of plants within homogeneous plant communities the following problem may serve as a starting point: Within a homogeneous plant community test areas of given size are placed and the number of individuals of a certain plant species falling within each test area are counted. The probability to catch a certain number, t, within a test area must follow some statistical law provided the individuals are distributed at random. Which law?

This teoretical problem must be solved to serve as a basis of judgement when valuing observations on the distribution of plant species in homogeneous plant communities in nature. If the statistical sequence follows this law the individuals may be distributed at random. If the observations cannot be represented by the theoretical series the individuals are not distributed at random and one may seek for explanations why it is not so.

There has been some discussion which type of distribution should be applied in this case. THE SVEDBERG (1922) assumes that the Poisson type of distribution should be applied. The binomial type of distribution may come in question, and OTTESTAD (1934) assumes on theoretical reasons that the hypergeometric type of distribution should be applied.

It is for the coming developments most convenient to use the same starting point as OTTESTAD. Suppose we have a limited plant community with n individuals of a certain species distributed at random. If we take out a test area of size x, in how many cases will t individuals of the species in question fall within the test area.

OTTESTAD thinks the community divided into elementary areas so many that none of them contains two individuals. Within the whole community there are B elementary areas and within each test area there are b elementary areas. In n of the elementary areas there is an individual of the species in question. We may now count B, b, n and t in terms of one unit and can transform the problem to one well known within mathematical statistics: If we have a sack containing B units of which n are marked and B—n not marked and we take out b units at random, in how many cases will we get t marked and b—t not marked units. This function is expressed by the hypergeometrical frequence function

$$h(t) = \frac{\binom{n}{t}\binom{B-n}{b-t}}{\binom{B}{b}}$$

On these reasons OTTESTAD assumes that this frequence function should be applied when valuing the distribution of individuals of plant species in natural communities.

In this case the whole community and the test area are measured in terms of an elementary unit. It is of importance to find out which formula should be applied if the test area and the community are measured in terms of quantity. The following symbols are applied:

a is the size of the community (e. g. in m^2),
B is the number of elementary units in the community,
x is the size of the test area,
b is the number of elementary units within the test area,
n is the number of individuals within the community,
p is the size of an ele [illegible]
k is the average living [illegible] e species in question, i. e.

$$k = \frac{a}{n}$$

Consequently

$$Bp = a$$
$$bp = x$$

We introduce $s = \frac{1}{p}$ and insert in the formula

$$h(t) = \binom{n}{t} \frac{\binom{as-n}{xs-t}}{\binom{as}{xs}}$$

If we let $p \to 0$ i. e. $s \to \infty$ we find after some calculation

$$b(t) = \lim_{s \to \infty} h(t) = \binom{n}{t} \left(\frac{x}{a}\right)^{t} \left(1 - \frac{x}{a}\right)^{n-t}$$

This is the binomial type of distribution.

If we applie the principles of sampling analysis we may take our community as a sample of a universe of the same constitution as our community. To find out which formula should be applied in such an universe we introduce k.

$$n = \frac{a}{k}$$

$$b(t) = \binom{\frac{a}{k}}{t} \left(\frac{x}{a}\right)^{t} \left(1 - \frac{x}{a}\right)^{\frac{a}{k} - t}$$

$$p(t) = \lim_{a \quad \infty} b(t) = \frac{\left(\frac{x}{k}\right)^{t} e^{-\frac{x}{k}}}{t!}$$

This is the Poisson type of distribution.

It is thus proved that there is a connection between the three laws of distribution previously proposed. If they are applied at a sufficiently large area and in case of the hypergeometrical function with a small elementary unit, they must in practice give the same result. We will in the following apply the Poisson formula because it is the most convenient type.

The mean of the Poisson series is $\frac{x}{k}$ and the variance (square of the standard deviation) is identical to the mean. In our binomial series the mean is $n.\frac{x}{a} = \frac{x}{k}$ and the variance is $n.\frac{x}{a}\left(1 - \frac{x}{a}\right)$. The Poisson series and our binomial series have the same mean but not the same variance. The quotient between the variance of our binomial series and our Poisson series is $\left(1 - \frac{x}{a}\right)$. Thus it is seen that with increasing area of our community the variance of the binomial series approaches that of the Poisson series corresponding to the formula $1 - \frac{x}{a}$. If a community is analyzed which is 1000 times the size of the test area employed, the difference of variance between the Poisson series and the binomial series will be 1 pro mille.

We have tried to calculate how many individuals must be present within a community if the binomial formula shall give the same results as the Poisson series within 1 percent. We have found:

If

$m = \frac{x}{k} = \frac{nx}{a} = \frac{1}{2}$ $n = 200$ is sufficient
„ 1 400 „ „
„ 2 400 „ „
„ 4 600 „ „
„ 10 1000 „ „

The Poisson type of distribution has the characteristic that the mean is equal to the square of the standard deviation. This may be taken as a criterion whether a given statistical series follows the Poisson type of distribution. If the square of the standard deviation is significantly higher than the mean, this may be taken as an indication that the individuals are more irregularily distributed than corresponds to the Poisson distribution, if the square of the standard deviation is less than the mean, this is an indication that the individuals are more regularily distributed.

One of us has taken a statistical series which may illustrate this. In an apparently homogeneous area of a *Sphagnum* bog with *Eriophorum angustifolium* as the dominating species, a statistical series of the number of shoots of *Eriophorum angustifolium* caught within test areas of 1 dm^2 was taken. The bog is situated at an altitude of 1100 m in Norway: Hemsedal: Kjølen above Markegardseter. The results are given below.

Sample no.	0	1	2	3	4	5	6	7	m	s^2	m—s^2
1—50	8	19	13	8	2				1.54	1.15	0.39
51—100	7	7	19	11	6				2.04	1.43	0.61
101—150	7	16	10	10	4	3			1.94	1.98	-0.04
151—200	6	5	17	17	4		1		2.24	1.53	0.71
201—250	5	12	18	12	2			1	1.98	1.57	0.41
251—300	8	6	18	13	2	2	1		2.10	1.89	0.21
301—350	2	13	16	17	1	1			2.10	1.03	1.07
351—400	6	10	16	13	4	1			2.04	1.47	0.57
401—450	6	14	18	9	2	1			1.80	1.27	0.53
1—450	55	102	145	110	27	8	2	1	1.98	1.43	0.55

As will be seen from the above table the square of the standard deviation is almost always higher than the mean. If the difference $m - s^2$ is tested by the formula

$$t = \frac{M}{\sqrt{\frac{V}{n}}} \cdot$$

Where M is the mean of the observations on $m - s^2$ and V the corresponding square of standard deviation, t is found to be 4.81. In this case f is 8. From the table of t will be seen that the probability that $m - s^2$ is 0 is somewhat higher than 0.001 and much less than 0.01. There is thus a statistically significant difference between the m's and the corresponding s^2.

If the series of observations 1—450 is compared with a Poisson series with the same mean, by means of the Chi quadrat method a Chi quadrat of 29.76 is found. f is here 5. Consequently the probability that this series can reasonably be represented by a Poisson series is less than 0.001.

This result may easily be given a biological explanation. If the individuals were distributed at random one would with intervals find areas with many individuals and also large areas without individuals. But on account of the competition, many individuals of *Eriphorum angustifolium* can hardly thrive in too close association, and if areas are free from individuals, some individual would probably grow up in the open space. This tends towards a more regular distribution than might be expected if the individuals were distributed at random.

Similar statistics have been published many times before. One point of importance should however be pointed out. Such statistics should always be carried out with the aid of a trained sociologist who knows something about the vegetation types in question and their ecology. Otherwise one may come across what has been called mosaics which may cause complications. Mosaics are close patterns of different vegetation types in one locality. An example may be given from the mountain plains south of Rondane in Central Norway. On these plains a vegetation of *Juniperus communis* shrubs is met with. The individuals of *Juniperus* seems to be quite regularily distributed, and the density of individuals is probably a function of the root competition; there is always some open space between the individuals.

In winter some snow always accumulates around the *Juniperus* shrubs. Thus the vegetation under the shrubs have a better snowcover in winter than it has the vegetation between. If a statistical series of the distribution of e. g. *Vaccinium myrtillus* was taken in this type of vegetation, one would certainly find a very irregular type of distribution.

One may conclude that two different vegetation types are present in this case because they can be reckognized from other localities where they are found in zones around the snowfields. In such vegetation they may occur in homogeneous stands.

Perhaps factors of this kind may account for the really astonishing result that in most cases when the distribution of plant species in apparently homogeneous vegetation types have been investigated, a distribution more irregular than corresponds to the Poisson formula has been found (ASHBY 1948). This may be an indication that factors of importance to the plant species under investigation have not been constant all over the area.

In phytosociological analysis it is common to state whether a species is present within a certain test area; countings of the number of individuals are more rarely made. Thus the probability to catch some individual of the plant species in question as a function of the size of the test area and the density of the species is of interest. In case of normal dispersion this probability, α, is

$$\alpha = 1 - p(0) = 1 - e^{-\frac{x}{k}}$$

This result has previously been reached by KYLIN (1925).

If the individuals of a species within a homogeneous plant community are more regularily distributed than corresponds to normal dispersion, not only the type of dispersion but also the shape of the test area will influence the statistics. This may easily be proved in case of a dispersion where the individuals are placed in the gitterpoints of a quadratic gitter. Applying a test area in the shape of a circle, the area of the circle must be 1.57 k to make $\alpha = 1$. Using a test area of square shape the corresponding area is 2. k.

These difficulties may be overcome by using test areas of a very irregular shape. The more irregular the shape of the test area, the more the dispersion type will approach the Poisson type.

The best way of making irregular test areas is to use a small elementary areas and for the larger areas use combinations of many elementary areas. But if this division is carried out in the extreme and the areas constituting the larger areas are selected at random from all parts of the community, it can be shown that the dispersion will approach the Poisson series by any type of dispersion even an inhomogeneous dispersion. In this case we will have no information about the dispersion at all. The elementary areas constituting the larger areas should be selected from the same part of the community.

Our statistical series from the *Eriophorum* bog as well as some previously published (SVEDBERG 1922, OTTESTAD 1934) shows types of dispersion somewhat but not very different from the normal. Under these conditions (employment of irregular test areas in case of very regular or irregular types of dispersion) the formula

$$a = 1 - e^{\frac{-x}{k}}$$

holds good with sufficient approximation for our further use.

In an homogeneous plant community it may be of interest to find out how the number of species caught within a test area is a function of the size of the test area. Such curves are of interest i. a. to find out how large test areas must be applied to make representative samples of the communities in question.

If such a curve is constructed from observations on natural homogeneous plant communities the result indicates that the number of species increases rapidly with the size of the test area for small test areas. By large areas, however, the curve is more flattened after a more or less marked inflexion point. At large areas the number of species increases no more with increasing test area, as long as one keeps within the limits of the same vegetation type. The area corresponding to the inflexion point, or the area corresponding to a number of species of 80 percent of the total of the community, is called the minimi area of the community. It is reckoned that a sample of at least the size of the minimi area must be taken to give a representative picture of a community in nature.

It is possible theoretically to find out how such a curve must look out in an homogeneous plant community with a limited number of species after the definition of homogeneity given above, provided the density of each species is known and the distribution of each species is approximately normal. For the first species we have

$$a_1 = 1 - e^{-\frac{x}{k_1}}$$

For a species, t, we have

$$a_t = 1 - e^{-\frac{x}{k_t}}$$

If the total number of species is n, we find that the total number of species caught in a test area of x square metres is

$$Y = n - \left(e^{-\frac{x}{k_1}} + e^{-\frac{x}{k_2}} + \;.....\; ...+ e^{-\frac{x}{k_n}}\right)$$

(KYLIN 1925).

This function has its mathematical characteristics. It approaches asymptotically the value n if x is exceeding all values. The first derivative is positive for all values of x and the second derivative is negative. The curve is consequently steadily rising for increasing x but the curvature is directed downwards. Thus the general outline of the curve is clear and well in accordance with the observations in nature.

Sometimes attempts have been made to approximate such „chance area" curves or „minimi area" curves as they have been called, by other mathematical functions. Any such statement must mean a statement about the distribution of the k's. But each community has its own set of species with each their own density. These can only be measured in nature and it is not very likely that it is possible to state much about their properties beforehand.

It is common among sociologists to divide the species of a community which has been analyzed by means of a test area of known size into different frequence classes (see e. g. Braun Blanquet 1928, Du Rietz 1930). The species occurring in between 80 and 100 percent of the samples are collected in the class V, those in the region 60 to 80 percent in the class IV, those in the region 40 to 60 percent in the class III, those in the region 20 to 40 percent in the class II and those in the region 0 to 20 percent in the class I. It has been an interesting result of such investigations that the number of species in the class V in all good analyses is greater then that of the class IV provided the test area is sufficiently large (Raunkiaer 1934).

This is easy enough to understand from the formula of a, which shows these frequence classes in reality to be of unequal size (Nordhagen 1922). This may be demonstrated in the following way:

If we take a test area of the size x, we can find out the dimension of k of a certain species if the species shall fall within the group V. The maximum value of k is given by the formula

$$0.8 = 1 - e^{\frac{-x}{k}}$$
$$k = 0.49\ x.$$

If the species in question shall fall in the class V its corresponding k must be between 0 and 0.49 x.

In the same way we find that if a species shall fall in the class IV the k must be between 0.49 x and 0.83 x, for the class III the limits are 0.83 x and 1.49 x, for class II 1.49 x and 3.50 x, and for the class I between 3.50 x and ∞.

If we take as a unit for counting the area which each individual of the species has for itself, its living space, which must be of primary significance to the plants, we find the dimension of the class V 0.49 x, the class IV 0.34 x, the class III 0.66 x, the class II 2.01 x and the class I ∞.

If the number of k's pro argument x is constant or decreasing for increasing x but not faster than corresponds to the function

$$z = 1 - e^{\frac{-r}{x}} \text{ (r is a constant)}$$

the number of species of the classes must be

$$V > IV < III < II < I$$

Raunkiaer found through observations in nature

$$V > IV \lesseqgtr III < II < I$$

and generally $III > IV$.

When the number of k's pro argument x is decreasing with increasing x, the maximum of the class V will become more marked, the greater the test area. If the number of k's pro argument x is constant, the maximum of the class V will not become more marked with increasing x, a result already obtained by **Romell** (1925).

If the number of species of the community is a limited one it is easy enough to prove that with any distribution of the k's there will be a maximum in the class V if the size of the test area is chosen sufficiently high. This is in the opinion of the authors the case of natural communities.

Now we turn to the synthetic conception — the association. Out of analyses of different homogeneous communities we build up the association. Now we are talking about more or less homogeneous associations, or more correctly spoken, about more or less homogeneous material for building up the concept of the association. We may define the homogeneity of the association in the following way.

An association is homogeneous when the local plant communities from which it has been built up, if placed together would form a homogeneous plant community after the definition of homogeneity of a plant community given before.

Now the associations are never fully homogeneous as are the local communities. We may then talk about more or less homogeneous associations. For controle of the homogeneity of the association we have the distribution of the species in different constance classes (see e. g. **Braun Blanquet** 1928), as we have the distribution of the species in frequence classes in the local community. It is clear enough that, when taking our definition of homogeneity of the association, the distribution of species in constance classes of the association must be the same as in the frequence classes of the local communities when the association is fully homogeneous and we use equivalent test areas from the different local communities. Now the associations are never fully homogeneous, but the curve must keep many of its characteristics, especially the maximum of the class V. In reality in very many homogeneous associations we find.

V > IV < III < II < I

The maximum of the class V is most important when valuing the homogeneity of the material from which different sociologists build up their units of vegetation although no absolute criterion (ROMELL 1925). A maximum of the class V does not prove that the material is homogeneous, but if the association is homogeneous the maximum of the class V must exist provided representative samples are taken from each community and the association contains a limited number of species. DU RIETZ always found V> IV in homogeneous plant communities if he used sufficiently large test areas. In most of the associations of the Zürich-Montpellier school at that date had V < IV. That brought DU RIETZ to the conclusion that the Zürich-Montpellier unit of vegetation (the association) was something essentially different from his homogeneous plant society, which he after agreement with Scandinavian as well as Zürich-Montpellier phytosociologists called sociation. This has led to an even more marked separation between the Zürich-Montpellier school of phytosociologists and the Scandinavian one, and has even in some cases led to the really remarkable conclusion that in the Alps the units of vegetation were something essentially different from those of the Scandinavian mountains.

The existence of two different schools with different methods and terminology was accepted by the Sixth International Botanical Congress whose Geobotanical Section passed the following resolution:

The Geobotanical Section of the Sixth International Botanical Congress recommends:

1. to use the term Sociation for vegetation units characterized mainly by dominance in the different layers in the sense of the Scandinavian plant sociologists;

2. to use the term Association for vegetation units characterized mainly by characteristic and differential species in the sense of the Zürich-Montpellier plant sociologists, or at least for units of the same order of value.

In the opinion of the plant sociologists of the Zürich-Montpellier school and after their experience the association should be applied as the basic unit of the phytosociological system. The sociologists of the Scandinavian school had a similar opinion about the sociation. Thus the definition, consciously or unconsciously applied by the sociologists were:

The Scandinavian School: The sociation is to be the fundamental unit of the phytosociological system and this is to be characterized mainly by dominance in the different layers.

The Zürich-Montpellier School: The association is to be the fundamental unit of the phytosociological system and this is to be characterized mainly by characteristic and differential species.

It will from these definitions be apparent that they consists of conjunctions of two different meanings. But it is by no means certain that it in all cases will be convenient to apply a fundamental unit of the phytosociological system which can be defined by means of characteristic species e. g. within specialized vegetation types with few species. On the other hand it may happen that dominance may be an inconvenient character to apply for definition of the fundamental units within vegetation types which are rich in species. Which methods should be applied must vary with the vegetation types under investigation and cannot a priori be stated.

In this connection it has been an interesting feature that the different methods when applied on similar vegetation types have given results which are remarkably consistent. Thus many association tables from Central Europe exhibit a very marked maximum in the class V. The correspondence in the units of vegetation published by KRAJINA (1933) from Tatra (using the term association) and by NORDHAGEN (1936) from the Scandinavian mountains (using the term sociation) is striking. It happens that Scandinavian authors publish sociation tables with class V < IV. All these examples indicate that the difference between the units sociation and association as these concepts are applied by many modern students is much of a formal and traditional nature. On reasons of priority we therefore prefer to use the term association for the fundamental unit of the phytosociological system.

We will give our opinion on the definition and properties of the association [cf. also DAHL & HADAČ (1941). HADAČ (1946)].

Definition: The fundamental unit of the phytosociological system is the association.

The association is a type of a plant community which occur repeatedly in different localities. The plant species of the communities of an association have approximately the same requirements to the environments, and are commensals i. e. they take their nutrition from the same source and in approximately the same way.

Properties: The individuals of plant species of communities belonging to an association influence their medium. This action, together with competition, creates distinct borders towards communities belonging to other associations.

The borders are usually sharp between communities belonging to floristically more different associations, less distinct between communities belonging to floristically more related associations. In stabilized communities the borders are generally distinct, between communities of the initial stages of the development of a new vegetation they are hardly recognizable. When borders between communities belonging to different associations are indistinct, this is often a sign of immaturity, lost equilibrium or degradation.

Within the borders of a community belonging to an association, the individuals are (more or less) homogeneously distributed.

Between the individuals of the species of communities belonging to an association there are interrelations. Thus the communities have the property in common with the organisms that a factor influencing one of its elements exercizes influence upon the whole community.

There are not only terminological differences between the Scandinavian school and the Zürich-Montpellier school, there are also difference in methods.

Most Central European sociologists have, really or apparently, neglected the problem of homogeneity of plant communities being more interested in ecology than in statistics. Scandinavian botanists have, on the contrary, especially studied the structure of plant communities. Thus they have, according to their interests, applied different methods of field investigation.

Central European sociologists work with large test areas, larger than the minimi area of the community, of variable size and shape and only one sample from each locality. Scandinavian sociologists applied, and still apply, much time and energy to find the most precise and objective method for the description of vegetation. These investigations have resulted in a series of different methods such as RAUNKIAER'S „valence method", line taxation methods, and the square metre method. At present the last one is most extensively applied. For the investigation of vegetation areas of 1 or 4 square metres in simple vegetation types, 16 sq. m. in complicated wood communities are chosen and carefully described. For the investigation of one community only one kind of square samples is applied. For the description of a community so many samples must be taken to obtain a representative total sample, i. e. that the sum of the sample areas is larger than the minimi area of the community in question.

It may be a matter of discussion which method is the most profitable for the sociological analysis of the vegetation. They have both their advantages and disadvantages. By means of the Scandinavian method it is possible to obtain a rough estimation of the k's of the species of the community in question. This cannot easily be made by the Central European method. Scandinavian sociologists are more interested in dominance and abundance of species of the communities than are the sociologists of the Central European school. The Central European method is quicker than the Scandinavian one and the full publication of the results require less space in print. Thus it is with the same amount of work possible to investigate more local communities by the Central European method than by the Scandinavian.

It has been advocated that the Scandinavian method alone has the advantage to be a statistical method. In our opinion none of the methods as they are applied by the vaste majority of the sociologists are statistical methods. There are the following reasons for this opinion.

By the selection of the patches of vegetation each sociologist chooses to analyze, a subjective element is introduced. No sociologist analyzes every local community he comes across, he chooses certain local communities because he believes them to be typical of a certain vegetation type or otherwise renders features of special interest.

Almost every local community is different from others belonging to the same sociological unit. This is evident from very many analyses published by Scandinavian sociologists. But very rarely so many samples are taken from a local community to permit a statistical analysis of the results, rarely more than 10 squares are analyzed. Often the local communities are too small to make a statistical analysis possible.

Sociologists applying the Scandinavian method for description of vegetation make no attempt of a statistical evaluation of the results. They calculate a K percent and a F percent, but any estimation within which limits these figures are statistically significant are never made.

In our opinion neither the Scandinavian school nor the Zürich-Montpellier school can claim to apply statistical methods by their description of sociological units. The methods of analysis is no more than a standardized method of description of vegetation which permits a qualitative comparison of the results. When a sociologist describes a new association this is done essentially after the same principles as a Linnean systematist describes a new species. Methods comparable to those of biometrical taxonomy have not as yet been introduced in sociology.

This is in itself no objection to the methods. By them it is possible to obtain information about vegetation and ecology which hardly can be obtained so easily by other methods.

It is an observation of some importance that the minimi areas of communities belonging to the same sociological unit may vary within certain limits. The minimi area of a community depends upon the densities of the species. The density of the individuals of a certain species depends inter alia upon the fertility of the soil. Thus historical factors (succession) are of importance. It is evident — as different local communities can have different age and consequently different stages of development and as there can be differences in the supply of nutrient salts in the medium of different local communities — the minimi area may vary within certain limits even if the floristic composition of the communities is very near the same. If one of two communities belonging to the same sociological unit has a minimi area of 3 sq. m. the other of 5 sq. m. we obtain in a test area of 4 sq. m. in the first community e. g. 90 percent of its species in the other only 60 percent. Examples of this are easily found in many sociological analyses published by Scandinavian authors.

Such observations may be of importance if we want to investigate the effect of historical factors upon the substratum or factors of fertility of the soil upon the minimi areas of the communities. But for the general description of the vegetation the test areas of 4 sq. m. are not equivalent. A factor often used by Scandinavian sociologists viz. the average number of species caught within the test areas cannot be correctly judged without the background of knowledge of the minimi areas of the communities.

Sociologists applying the Central European methods of description of vegetation always take areas larger than the minimi areas. Such test areas are equivalent even if the areas are of unequal size.

SUMMARY.

Arguments are given for the opinion that the homogeneity of plant communities and the discontinuities between local communities are caused by competition between the individuals of plant species and by their power to influence their own milieu. Mathematical calculations are made on homogeneous communities which explain some of the characteristics of the constance and frequence curves and the curve of relation between the number of species caught within a test area and the size of the area. The results confirm that frequency and constancy curves may be used as criteria of the homogeneity of the local communities and associations. A statistical series from an *Eriophorum anqustifolium* bog is published and the results indicate that the individuals are more regularily dispersed than expected if the individuals were distributed at random.

The relations between Zürich-Montpellier and the Scandinavian schools of sociologists are discussed. It is the opinion of the authors that the sociation of the Scandinavian school

and the association of the Central European both are designed, consciously or unconsciously, to be the fundamental unit of the phytosociological system. By which criteria this fundamental unit should be characterized ought to be decided in each case and cannot a priori be stated. As the concepts of sociation and association are applied by many modern sociologists the difference is more of formal than of a real nature. It is proposed to use the term association for the fundamental unit without statements by which criteria it should be characterized.

The methods of analysis of vegetation of the Scandinavian and Zürich-Montpellier schools are discussed. It is emphasized that none of them are of a statistical nature and that perhaps for the general description of vegetation the Zürich-Montpellier method has some advantage.

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